Biological Invasions in Europe and the Mediterranean Basin

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Biological Invasions in Europe and the Mediterranean Basin

Edited by

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Preface

In view of the massive change in the area of distribution of many world biota across classical biogeographical realms, and of the drastic restructuring of the biotic components of numerous ecosystems, the Scientific Committee on Problems of the Environment (SCOPE) decided at its general Assembly in Ottawa, Canada, in 1982 to launch a project on the 'Ecology of Biological Invasions'.

Several regional meetings were subsequently organized within the framework of SCOPE, in order to single out the peculiarities of the invasions that took place in each region, the behaviour of their invasive species and the invasibility of their ecosystems. Most noteworthy among such workshops were one in Australia in August 1984, one concerning North America and Hawaii in October 1984, and one dealing with southern Africa in November 1985.

A leitmotiv of these workshops was that most of the invasive species to those regions were emanating from Europe and the Mediterranean Basin, inadvertently or intentionally introduced by man. It was therefore considered as a timely endeavour to organize the next regional meeting in relation to this region.

The workshop on 'Biological Invasions in Europe and the Mediterranean Basin' was held in Montpellier, France, 21 to 23 May 1986, thanks to the financial support of SCOPE and of the A.W. Mellon Foundation, and the logistic facilities of the Centre National de la Recherche Scientifique (C.N.R.S.). It was not organized as a formal and large conference with presentation of well-structured papers. Rather, a small number of invitees, envisaged as being authors of chapters of the foreseen synthesis book, presented draft introductions on different topics with the purpose of stimulating discussion with a selected group of participants. Therefore, this volume does not represent the proceedings of the Montpellier workshop. All chapters were elaborated long after the workshop, but taking into due account the insights from the discussion. Furthermore, a few other authors were selected later on to fill evident thematic gaps.

The book comprises 27 chapters. After an introduction, 10 chapters deal with plant invasions, two of them from a paleoecological viewpoint; Fox's chapter extends the comparison to all regions of the world with a mediterranean-type climate. The 8 chapters on animal invasions cover different topics: invasions in ancient and recent times, invasions by vertebrates and invertebrates, invasions in terrestrial and in aquatic and marine environments; four chapters refer, to a varied extent, to invasion by parasites. Finally, 8 chapters approach the processes and mechanisms of invasion, from physiological, genetic and ecological viewpoints; while based on examples from Europe and the Mediterranean Basin, their considerations transcend the boundaries of the region.

The core of this volume is definitively on invasions towards and within Europe and the Mediterranean Basin. Nevertheless, many remarks and hypotheses are intended to help explain why species from this region have such a great invasion potential in relation to other continents.

Of course, a comprehensive treatment would have been impossible due to the extent and the heterogeneity of the region, and the multiplicity of taxa. Each chapter has to be considered as a kind of case study, illustrating problems of greater coverage and repercussions.

Finally, it is unquestionable that recent events linked with the increased human impact on ecosystems, the improved transportation systems, the driving forces of an internationally-wide market and trade economy, and also the impending man-made global climatic change will further promote a mix up of new species assemblages in the biosphere. It is hoped that this volume will contribute to the understandig of such complex and far-reaching phenomena.

F. di Castri   A.J. Hansen   M. Debussche

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PART ONE

Introduction

1. On invading species and invaded ecosystems: the interplay of historical chance and biological necessity

FRANCESCO DI CASTRI

Abstract.

The invasion by alien species of new regions and territories is a phenomenon of paramount importance, particularly in the last four centuries after the 'Great Discoveries'. Biological invasion is likely to acquire soon an even greater frequency, because of the current transportation systems and the forthcoming global climatic change.

'Invader' species have diverse sets of ecological, physiological, genetic and morphological characteristics that make them suitable for wide dispersion, colonization and competition. We refer to their intrinsic aptitude and potential for invasion as their 'biological necessity'.

Nevertheless, no one of the various sets of biological characteristics can fully explain success or failure to invade. It is indispensable for invaders to have caught opportunities to leave and to be transported, and to have found at their arrival open spaces, available resources and ecosystems poorly resistant to invasions. This is their 'historical chance'.

Among new patterns of invasion are those associated to the release of genetically designed organisms. Bioengineered organisms cannot be related to any of the existing biogeographical realms. A new world-wide 'anthropogenic realm', with its own peculiar characteristics and trends, is to be considered.

Introduction

It is a truism to say that human activities are changing the face of the world and that very few ecosystems, if any, are completely 'natural' in their species composition and functioning patterns. Acting as a *geological agent*, man has largely modified landscape composition, and is rapidly expanding an atypical ecosystem type, the urban one. As a *biogeographical agent*, by creating new habitats, new barriers and mostly new bridges, man has favoured new mixtures and assemblages of species, often belonging to previously distinct and separated biogeographical realms. Because of his new (and non-desired) role as a *climatic*

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agent, man is likely to produce the most unprecedented and rapid migration trends (as well as many extinctions) of all biota of the world.

Consequently, in the surroundings of human settlements and agricultural fields (and even in less modified habitats), our neighbouring plants and animals may represent a mosaic-like association of most of the biogeographical realms of the world.

The problem of the biological invasions, illustrated in a so captivating way by Elton in 1958, has already profound implications of high economic importance in such areas as agriculture and weeds control, biological control of pests, aquaculture and epidemiology (e.g. rabies control, see Bacon (1985); even the spread of AIDS can be considered as a peculiar case of biological invasion.

Moreover, exploring the mechanisms and processes related to biological invasions has *per se* high heuristic value, since it implies a 'meeting point' and a close interaction for ecologists, geneticists, population biologists, physiologists and evolutionists, agriculturists, parasitologists, and even historians like Braudel (1979) and Crosby (1986).

In particular, Crosby emphasizes the role played by Europe as a source from which many groups of biological invaders left to aggressively colonize other continents, often displacing local biota. He refers to this phenomenon as 'ecological imperialism'.

What is a biological invader?

A biological invader is a species of plant, animal or micro-organism which, most usually transported inadvertedly or intentionally by man, colonizes and spreads into new territories some distance from its home territory. Often, invaders spread from one biogeographical realm to another.

Classical examples of invaders are, for instance, the black rat, *Rattus rattus* (see Michaux *et al.* this volume), or the house sparrow, *Passer domesticus* (see Niethammer 1969), both clearly associated to man. Most likely emanating from Asia, they have progressively colonized Europe and from there all continents, being very common in the vicinity of most human settlements. Invaders can belong to most of the taxa; even large conifers such as *Pinus radiata* from California and *Pinus pinaster* from Europe are aggressive invaders of South African ecosystems (Macdonald *et al.* 1986).

Unavoidably, there are different viewpoints on the notion of a 'biological invader', as exemplified in Figure 1. The central overlapping zone of the four circles symbolizing the approach of biogeographers, ecologists, population biologists and geneticists, and practitioners, is intended to cover the definition and the characteristics of an invader. Nevertheless, no single approach embraces comprehensively the notion of invaders.

A biogeographer is primarily interested by the time of the invasion and the progressive spreading of the areas of distribution, while ecologists and

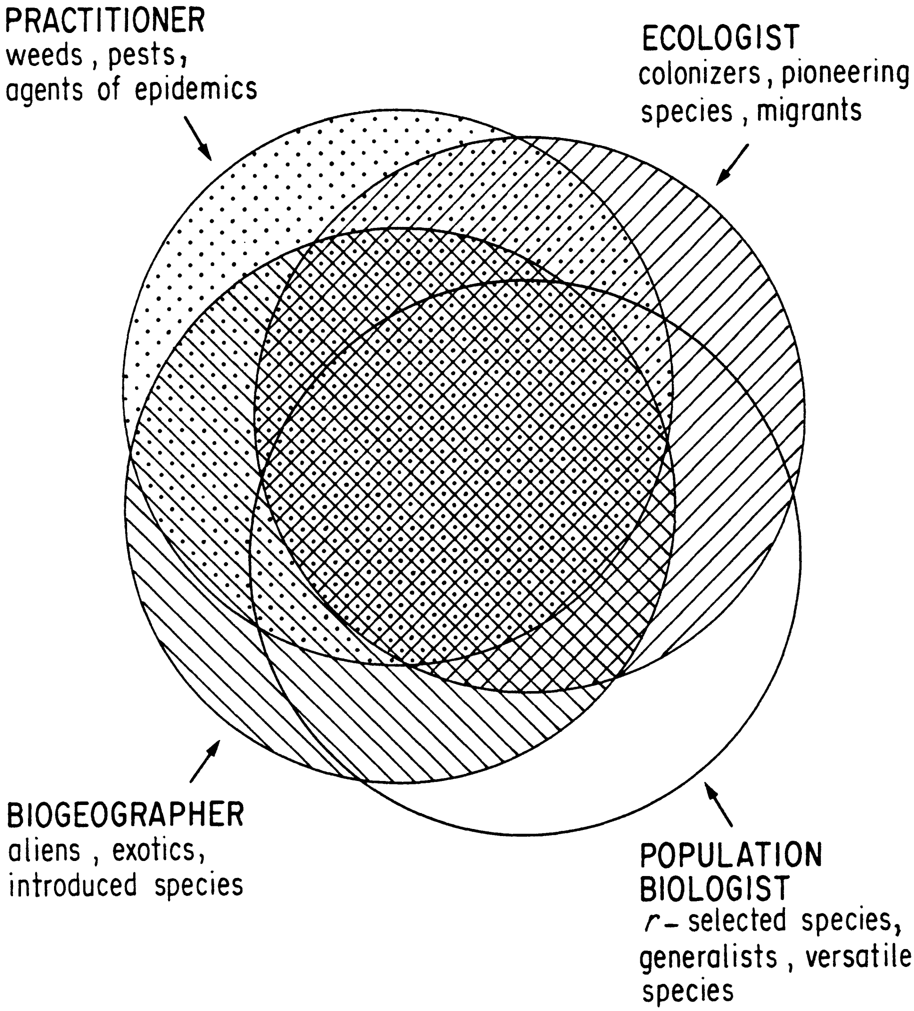

Figure 1. The symbolic overlapping and intercrossing of four approaches to cover the definition and the characteristics of a biological invader (after M. Rejmánek, personal communication, largely modified).

geneticists may concentrate their attention on the mechanisms and processes involved in these phenomena. The practitioner has necessarily in view the economic and health damage provoked by these invasions, as well as the measures of quarantine, preventive control or eradication to be taken as regards a given invader.

As a matter of fact, the 'invasion' term should be primarily used with a biogeographical connotation, but this is not always the case, not even in this volume. Incidentally, 'invader' is by no means synonymous of cosmopolitan species. Most of the invaders are not cosmopolitan; several cosmopolitans have not an invader behaviour.

According to different perceptions and research objectives, biological invasions can be studied at different hierarchical levels of space and time (hopefully by combining different scales), in consideration to the time of occurrence and spreading of the invasion or the distance from the originary territory of the invader. Figures 2 and 3 provide an overview of this scaling problem. Scales of space and time are given only as a very rough approximation. Attention should be drawn to the period of the Great Discoveries which has provoked *de facto* a breakdown of the biogeographical realms as well as a 'revolution' of the food customs all around the world.

The role of human history driving forces in the Old World as related to biological invasions has been treated in greater detail by di Castri (1989a), as has the importance of taking into account hierarchical scales when dealing with this kind of problems (di Castri and Hadley 1988). Practically all scales of space and time are approached in the different chapters of this volume.

The intermingled profile of a potential invader

At the present state of knowledge, it would be inappropriate to argue that there are specific sets of biological characteristics which could be considered

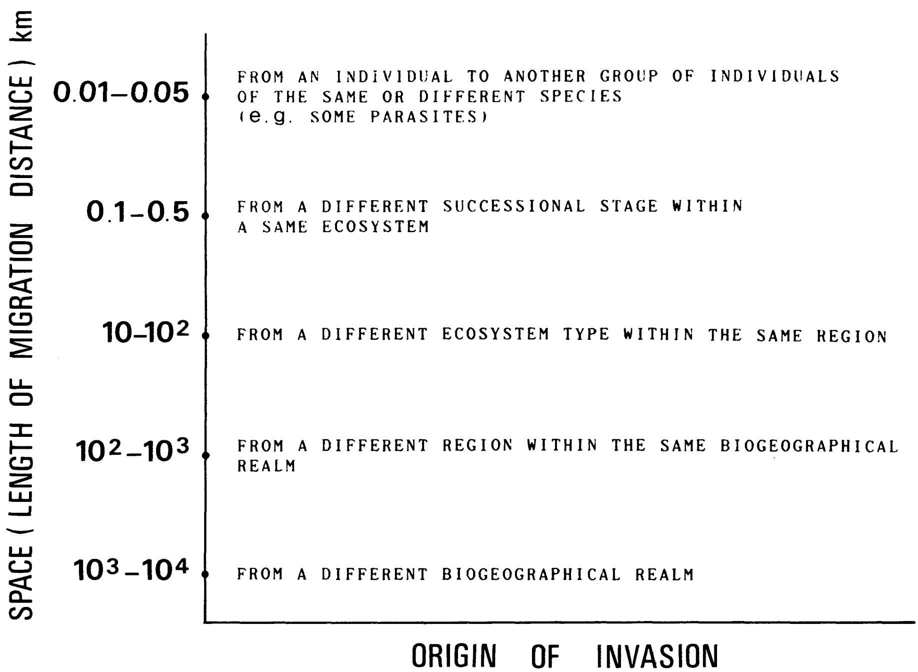

Figure 2. Scale of space as regards the distance from the place of origin of a given invasion.

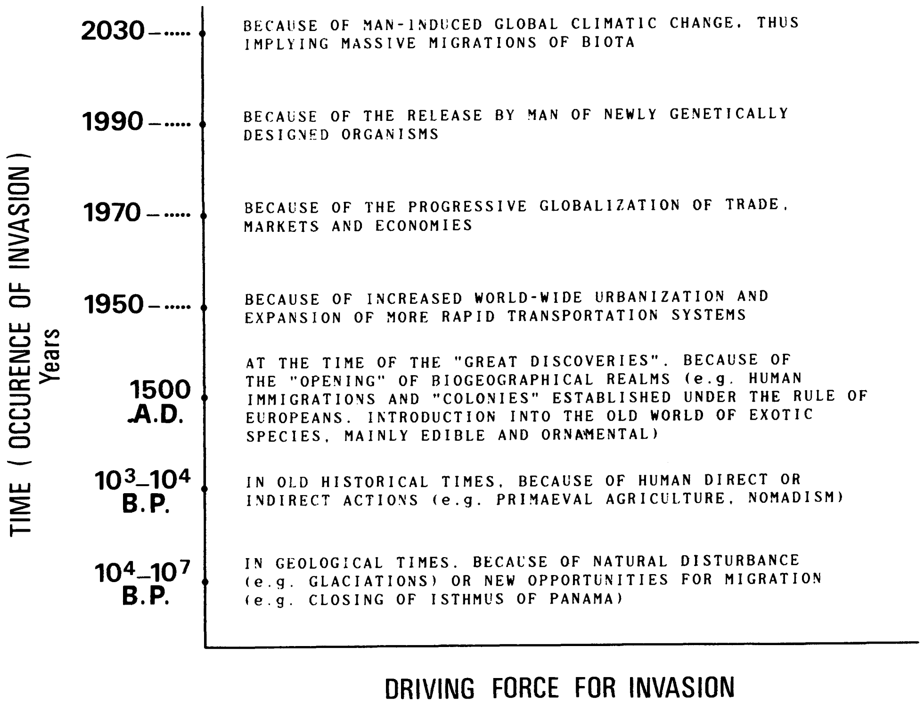

Figure 3. Scale of time as regards the initial driving forces for biological invasions.

strictly peculiar to the condition of being ‘an invader’.

Table 1 single out some biological attributes that are likely to facilitate the invasibility by given species of plants or animals. Roy’s chapter in this volume discusses in a more thorough and comprehensive way the characteristics of a plant invader (see also Baker 1965, Barrett and Richardson 1986, Newsome and Noble 1986).

Some of the attributes of Table 1 are quite obvious; for instance, morphological characteristics of seeds that facilitate transportation by wind, like the winged seeds of *Fraxinus*, *Ulmus* or *Acer*, or by animals such as the spiny seeds of *Xanthium* hanging up the skin or wool of large herbivores. In this respect, it is worth mentioning the monumental work of Thellung (1908–1910) who identified hundreds of adventive species near Montpellier, most of them introduced through the import, the hanging out and the drying of wool in Port-Juvénal. Some of these species are not still represented there, so that it would be very interesting to identify those definitively naturalized in the region, in order to quantify the difference between introduction/colonization and naturalization processes.

Admittedly, the attributes listed in Table 1 are very incomplete, some of them could be shifted from one column to another, or could appear in more than a single column. Nevertheless, they give room for some generalization:

Table 1. Some biological attributes of a possible invader.

Related to ecology and physiology	Related to morphology and behaviour	Related to genetics and population dynamics
Wide potential niche	Small body size	Subject to *r*-selection
Non-specialized germination and regeneration patterns	High mobility	High fecundity
Non-specialized pollination patterns	High vagility	High population growth
Dormancy	Apt to phoresis	Short and simple life-cycle
Rapid growth	High resistant spores	High genetic variation
High resource allocation to reproduction	Seed morphology (spiny seeds or burr, plumed seeds, winged seeds or samara) suitable to long dispersal by wind or animals	Uniparental reproduction
Longevity of seeds able to create seed banks		Polyploidy
Edible fruits and seeds transported by animals		

(a) No one species can possess all these attributes, but an unpredictable proportion of some of them.

(b) As regards possibilities of invasion, there are large differences between plants and highly mobile animals as mammals, birds or fishes, or small vagile organisms like Tardigrada, Rotifera, Nematoda, Fungi and Bacteria.

(c) Nevertheless, there are varied groupings of ecophysiological and genetic characteristics which seem to facilitate successful invasion (but not a single and stable grouping can be recognized).

(d) Conversely, species having many of these attributes have proved (up to now) not to be invaders. Even more, species having opposite attributes (e.g. highly specialized species, *K*-selected strategy species) have shown an invader behaviour.

For instance, in taxonomic groups of the same genus (e.g. *Rattus*, *Eichornia*, *Bromus*, etc.), some species have shown to be highly invasive, while other very related ones do not show any invader potential. It is a very challenging research topic to clarify why related species of the same genus reveal such a different behaviour. In other words, it is important not only to investigate why a species is an invader but also, equally relevant, why its closer relative *is not* an invader.

One can also wonder if the potential for invasion to a new territory has some correlation with the dispersal behaviour in the home region. There are examples leading to opposite conclusions. For instance, *Pinus pinaster* and *Pinus radiata* are both strongly invaders in South Africa (MacDonald *et al.* 1986), while only *Pinus pinaster* is slightly invasive in Southern France as compared with close species. *Pinus radiata*, on the contrary, has a quite restricted distribution in its home country, California.

In any event, one can stress that factors extrinsic to species biological attributes (e.g., historical opportunities or characteristics of the recipient ecosystems) are often the most important ones in determining the success of an invasion.

Finally, the mobility of modern society and the globalization of its functioning will probably change the characteristics of the 'ideal invader'.

The chance to be an invader

In line with some of the above paragraphs, this section will deal more with chance and historical opportunities than with intrinsic biological attributes. Disturbance will be a key-word; the meaning of endogenous or natural disturbance and of exogenous or man-made disturbance is that proposed by Fox & Fox (1986).

Table 2 summarizes the three main conditions; a kind of pre-adaptation acquired in the home country; the opportunity and the requisites to afford

Table 2. Conditions facilitating the potential to invade new territories.

Historical conditions in the home territory	Facilities for transportation and/or migration	Local conditions facilitating colonization by new invaders
Geological and evolutionary history of recent natural disturbance (e.g. glaciations, regional tectonic pulses, frosts, droughts)	Intensive exchanges of people and their products because of trade, colonization or war	Existence of open spaces and spare resources
Early man-related history of exogenous disturbance (e.g. grazing pressure by large herbivores, fires)	Rapid transportation systems	Ecosystems subject to frequent natural disturbances
Domestication by man and commensalism	High vagility of invaders	Man-disturbance of ecosystems similar to that of the home territory
	Phoresis (active transportation of small animals by larger insects, birds, etc.)	Absence of pathogens, parasites, predators, competitors left behind in the home territory
	Longevity of seeds, resistance of spores and possibility of long dispersal (by oceanic currents, wind, etc.)	Homoclimatic and mostly homocultural (similar land-use patterns) conditions as compared to home territory
		'Insularity' conditions (evolutionary history with isolation patterns) in islands, southernmost tips of continents (South America, South Africa, Australia) and western fringes of continents (e.g. Chile)

a long transportation; and the finding of non hostile conditions at the arrival to the new territories. Expressed in more anthropogenic terms, one can say: 'receiving a basic background open to alternative professions', 'catching the right ship' and 'becoming better competitor than the local species'. In all these steps, there is an interplay of chance and necessity, of human-derived opportunities and of evolutionary heritages.

It is undeniable that some of the conditions of the first and second columns are more applicable to species originating in Europe and the Mediterranean Basin, so that, in general, species from the Old World have a greater potential for invasion than those of the other continents (di Castri 1989a).

Some of the factors included in Table 2 are self-explanatory. I would like to put some emphasis only on a few points.

First of all, when man-made disturbances have similar effects than previous or concomitant natural disturbance in the same region, the pre-adaptive patterns are magnified. This is the case, for instance, of natural fires (and the selection for fire-adapted plants) followed later by man-made fires to open new spaces for agriculture and grazing; the grazing pressure by large wild herbivores, followed by grazing of domesticated animals; the alternative phases of clearing because of tectonic phenomena, killing frosts and extended droughts, followed later on by forest clearing by man to establish primaeval agricultural

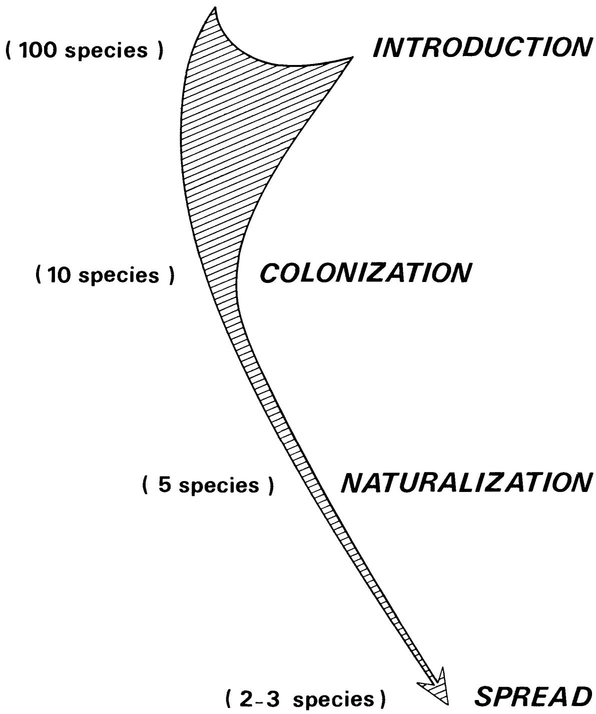

Figure 4. Main steps of a process of biological invasion, and the hypothetical loss of invading species at each step.

fields. The pre-adaptations because of this kind of natural/man-made 'relay' increase considerably the potential for invasion, mainly because the similarity between old and newly-established landscape patterns seems to have a greater relevance for invasion that the simple similarity of climates between the former and the new territories. In conclusion, invaders are favoured in new habitats when those habitats are subjected to disturbances that are novel to native species, but similar to those long experienced by the invading species.

Finally man, by multiplying the 'insularity' conditions throughout the fragmentation of land, further increases the chance for successful biological invasions. Island-like ecosystems are the most prone to be invaded.

Among the factors enumerated in Table 2, commensalism would be worth of a more extended discussion, as one of the most important conditions dealing with species dispersion and invasion related to man. As regards the common house mouse (*Mus musculus domesticus*), ecological and ethological processes are implied in the chromosomic differentiations between wild and commensal populations (Auffray *et al.* 1986, 1988, Bonhomme *et al.* 1983). Such aspects are further discussed in the chapter of Michaux *et al.* (this volume).

In any event, a simple introduction of a species in a given territory does not necessarily implies its naturalization and dispersal. On the contrary, its chance is rather limited as exemplified in Figure 4. It should be stressed, for instance, how few of the arthropods and other small animals falling down from the 'aerial plankton', after long-range transportation by wind, have a real possibility of colonization.

The natural resistance of ecosystems to biological invasions

It has been empirically observed that some regions or ecosystem types are more vulnerable than others as regards biological invasions. In addition, analogous ecosystems situated in different biogeographical regions show a different susceptibility to invasion. For instance, ecosystems from the Northern Hemisphere (mostly from the Old World) are more resistant than those of the Southern Hemisphere, particularly their southernmost parts. Timing of invasion has been also different in the various regions of the world.

Comparing the five regions of the world with a mediterranean-type climate (di Castri 1981, Fox, this volume), that is to say, the Mediterranean Basin, California, Chile, South Africa, South-Western and Southern Australia, ecosystems of the Mediterranean Basin are the most resistant to invasion, and even represent the home-country of most invaders to the other regions.

As a basis for intercontinental and inter-region comparisons on invasibility, see Drake *et al.* 1989, Duffey 1988, Groves & Burdon 1986, Kornberg & Williamson 1987, Macdonald *et al.* 1986, Mooney & Drake 1986, Sauer 1988, Wilson & Graham 1983.

Patterns of disturbance regime and degrees of biogeographical isolation during ecosystems evolution (di Castri 1989b) are the two main factors to explain such differences.

It has been postulated that no invasion can occur without a previous disturbance of the recipient ecosystem (Fox & Fox, 1986, see also Kornas, this volume). I tend to agree, so far it is accepted that there are so subtle alterations that are badly perceivable by man, and that species introduction can represent *per se* a disturbance. According to the disturbance hypothesis, ecosystems subjected to irregular massive disturbances (floods, killing frost, etc.) and to episodic extreme events are very susceptible to invasion; ecosystems with recurrent disturbance are prone to invasion, while those free from disturbance (but this is a biological abstraction) or with low-intensity disturbance are invasion-resistant. Nevertheless, it is important to differentiate between the long-term disturbance regime and the disturbance regime in place at the time of invasion; the most invasion-prone system may be one where disturbance is traditionally mild and infrequent, but where new forces cause intense and frequent disturbances.

Following the species richness hypothesis (Fox & Fox 1986) on the way that rich communities would be less susceptible to invasion, communities with many interacting species and high interconnectedness would be better suited to fully utilize existing resources, and therefore able to prevent new species to become involved. It seems an acceptable speculation, but there are little experimental data to prove or disprove this hypothesis.

As a matter of fact, it happens that species of *Hakea* from Australia as well as Northern Hemisphere *Pinus* (e.g. *pinaster*, *radiata*) are able to invade natural ecosystems with high diversity in Southern Africa (Macdonald *et al.* 1986). In Europe, close natural (or almost natural) forest ecosystems are very resistant to biological invasions, and very few exceptions can be quoted (see Kornas, this volume). Susceptibility to invasion sharply increases under conditions of stress, for instance, because of acid rains.

Riverine and riparian ecosystems, where intermediate to high disturbance regime is an intrinsic feature, are more easily invasible; fishes from South-Eastern North America such as *Gambusia affinis*, from North America as for instance *Ameiurus nebulosus* and *Salmo gairdneri* (rainbow trout) have been successful invaders, among others, as well as *Ondatra zibethica* (the North American muskrat) and *Myocastor coypus* from South America. Coastal and urbanized environments – the most disturbed ecosystems – show a profusion of invaders.

Most of the biological invasions to Europe, and certainly the most conspicuous ones (*Rattus rattus, Rattus norvegicus, Mus musculus, Passer domesticus*, etc.) come from the East (including the Far East); incidentally, most of the human migrations and invasions in historical times show the same East-West direction. Also neolithization, with all the cortège of associated plants and animals, appeared some 4.000 years earlier in the Eastern Mediterranean, shifting slowly towards the Western Mediterranean (Le Houérou, 1981). Many of the old migrations of Coleoptera (see Marcuzzi, this volume) are in a South-North direction in the Mediterranean.